

SACCOGLOSSUS APANTESIS, A NEW SPECIES OF ENTEROPNEUST FROM SOUTH AUSTRALIA

By I. M. THOMAS*

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SUMMARY

A new species of the enteropneust genus *Saccoglossus* is described and named *Saccoglossus apantesis*. This is the first record of this genus in Australia and the first enteropneust to be described from South Australia.

I. INTRODUCTION

Enteropneusts already recorded from the Australian continent include *Balanoglossus australiensis* (Hill) found near Sydney (Hill, 1894); *Ptychodera flava* Escholtz (= *Pt. pelsarti*), from the Abrolhos Islands (Dakin, 1916), and *P. flava* and *B. carnosus* (Willey) from the Great Barrier Reef (Trewavas, 1931). Trewavas also described a number of tornaria larvae from the same region which have not yet been associated with specific adults. The present author has identified a single specimen sent to him from the Great Barrier Reef as *Glossobalanus hedleyi* (Hill) first described from Funafuti (Hill, 1897). In 1899 Benham described *Saccoglossus otagoensis* (Benham) from Otago Harbour, New Zealand.

The form to be described herein is found on the shores of Encounter Bay, South Australia (lat. 35° 35' South, long. 138° 36' East) about fifty miles due south of Adelaide. The foreshore in this region consists of an extensive platform of a sandy Permian fluvioglacial stratum. The platform extends about one hundred yards offshore, sloping gradually seawards and dropping abruptly into deeper water at its outer edge. It is largely overlaid by a deposit of coarse sand, shell grit and some mud, which supports a thick growth of *Posidonia*, *Cymodocea* and *Zostera*. The first two of these plants cover most of the platform, whilst the latter is found in shallow water near its shorewards edge. Here the rock surface is pitted and dented to form basin-shaped depressions where the soil may lie to a depth of six to twelve inches, though in much of the area investigated the soil is no more than half this depth. This part of the coast is protected in part, to the west by Rosetta Head ("The Bluff") and offshore, to the south, by Wright Island, about half a mile away. Both these are granitic outcrops. The region is thus normally one of more or less quiet water.

The animals are found in the upper two or three inches of soil which is lightly bonded by *Zostera* roots. They have not as yet been found other than in association with this plant. Other animals found in the same habitat include Maldanid and other polychaete worms, some burrowing crustacea (*Callinassa ceramica* and *Crangon novozelandiae*), several burrowing lamellibranchs and occasional sipunculids and nemertines. The enteropneusts are extremely localised in their distribution. Although a considerable area of the foreshore has been examined by digging and sieving, they have been found only in three small regions, each not more than two square yards in extent and all about the same distance from high water mark. The regions are exposed at very low spring tides. The restricted distribution of the animals might be accounted for by

* Department of Zoology, University of Adelaide.

the pitted nature of the underlying rock which might tend to limit their lateral movements. In these regions, however, several specimens can be turned up in a single spadeful of soil. The animals are frequently so tangled in with the *Zostera* root-systems that it is almost impossible to obtain complete specimens. The abdominal region in particular is very fragile and breaks off readily. Brambell and Cole (1939a) have recorded that it is impossible to obtain intact specimens of *Saccoglossus cambrensis* because of its fragility.

A single specimen has been found in a similar habitat at Salt Creek near Edithburg on the eastern coast of Yorke Peninsula. Though this example was not sectioned, it bore all the external characteristics of the Encounter Bay specimens. Salt Creek is, in a direct line, about sixty miles north-west of Encounter Bay so it is likely that further investigation of suitable localities may show the animal to have a wide distribution along the South Australian coastline.

When the water is very still, casts can be seen on the sand surface which are similar to those produced by *S. cambrensis* (Brambell and Cole, 1939a). They are in the form of fine coils of sandy material bonded together by mucus. They are about a centimetre in diameter and one to one and a half turns in length and very fragile. No tubes have been observed though, if present and fragile, as are the castings, they would be no doubt shattered among the *Zostera* roots in the process of digging and sieving.

The following features place the animals in the family *Harrimaniidae* Spengel: (a) lack of hepatic diverticula, (b) lack of synapticalae, (c) lack of lateral septa, and (d) lack of circular muscles in the trunk region. They agree with the diagnosis of the genus *Saccoglossus* Schimkewitsch (= *Dolichoglossus* Spengel) in the following points: (a) proboscis very long, (b) collar about as long as broad, (c) lateral genital ridges present but no dorsal gonads, (d) gonads overlap the genital region to some extent, and (e) gill pores small but distinct. The specimens differ in several points from the published descriptions of the fourteen other species of the genus, so it is proposed to erect a new species, *Saccoglossus apantesis*, to include them. The specific name is derived from the Greek word meaning a meeting or an encounter, as it was near the place where the animals were first found that there occurred the historic encounter between Matthew Flinders in the "Investigator" and Nicolas Baudin in the "Geographe" in April, 1802.

Several detailed accounts of the anatomy of different species of the genus are available apart from the compendium of van der Horst (1927-39), for example, *S. otagoensis* by Benham (1899); *S. inhacensis* by Kapelus (1936); *S. cambrensis* by Brambell and Cole (1939a), and *S. horsti* by Brambell and Goodheart (1941). In the description of the present species then, only those features which are characteristic of *S. apantesis* will be dealt with. Features which it shares with several other members of the genus will, in the main, be omitted.

II. EXTERNAL FEATURES

S. apantesis is a moderately sized species. An adult in the living condition has a length of 70 to 85 mm. This is made up as follows: proboscis 20 to 25 mm.; collar 3.0 to 3.5 mm.; branchial region 10 to 12 mm.; genital region 15 to 20 mm. (the two latter regions overlap to a considerable extent); abdominal region 25 to 30 mm. The genital region in mature specimens is always coiled so that the measurements given for this region can be no more than an estimate.

Young specimens are coloured a uniform light orange. Adults have a proboscis of light orange, darkening somewhat at the base and stalk. The collar is orange-red with, in larger specimens, a white ring near the posterior margin. The branchial region is paler than the collar though darker than the proboscis. In females the genital ridges are light orange, but in males they are brownish red. The lateral and ventral body walls in the genital region are similar in colour

to the branchial region. The abdominal region is pale yellow-grey and translucent so that its enclosed sand grains and grit show readily through. No spotting or flecking with colour such as has been described in some other members of the genus is present.

The proboscis, in the extended condition, tapers from its base to its tip, the tip being about half the diameter of the base. In contracted specimens it is cylindrical. There is only a very slight indication of a dorsal groove in the posterior quarter or so of its length and this is better seen in preserved and contracted material than it is in living specimens. There is no sign of a ventral proboscis groove. Occasionally the proboscis may show one or more deep, circular constrictions at varying positions along its length. These are caused by strong local contractions of the circular muscles. If a specimen is roughly treated while the proboscis is in this condition, the organ may break at these points. Autotomy of this kind must occur in natural conditions as very occasional specimens have been found with short probosces showing signs of terminal regeneration.

At the base of the proboscis is the pre-oral ciliary organ whose structure and significance have been described for *S. cambrensis* and some other forms by Brambell and Cole (1939b). As in the Welsh species, it takes the form of a horse-shoe-shaped groove, slightly dilated at its free dorso-lateral ends and partially surrounding the base of the proboscis where it tapers to form the stalk. The organ is not distinctively coloured as it is in *S. cambrensis* and therein resembles more the condition in *S. horsti* (Brambell and Goodheart, 1941).

The neck which unites the proboscis to the collar is, as is the case in other members of the genus, very slender. It bears on its left side the single proboscis pore which enable the end sac (Fig. 1), and thus the left dorsal coelomic pouch of the proboscis, to communicate with the exterior. The collar is slightly longer dorsally than it is ventrally and is somewhat flared anteriorly. The posterior border is slightly flared also and at the base of this flare there is a conspicuous circular groove corresponding in position to the white ring mentioned earlier. This groove and white ring are best seen in mature specimens. The posterior flare overlaps the first two or three gill pores.

The branchial region possesses thirty to forty-five pairs of gill pores on its dorsal surface. The number apparently increases with increasing size of the animals. The anterior ones are small and almost circular. They increase in size to about the sixth pair of the series and become elliptical laterally. The final seven or eight become rapidly smaller and more circular in form, the ultimate ones frequently being difficult to discern externally. The latter part of the branchial region is overlapped by the genital region, the first genital pouch appearing usually at about the level of the twentieth pair of gill pores. It is noticeable that in less mature specimens, that is, those with a smaller number of gill pores and less well-developed gonads, the proportion of gill clefts in front of the first genital pouch is higher than it is in more mature specimens. This may be due to the combined effect of an increase in the number of branchial pores posteriorly and an anterior penetration of the gonads with increasing maturity. In mature specimens, the gonads form conspicuous dorso-lateral genital ridges which, in their region of maximal development, that is, in the posterior branchial and oesophageal regions, comprise about two-thirds of the animal's total body width (Fig. 8). The ridges begin to decrease gradually in size in the posterior oesophageal region and disappear in the anterior abdominal region. The increase in bulk of the genital ridges with growth of the animals to maturity leads to a considerable coiling in this part. Between the gill clefts, and farther back between the genital ridges, a slight medio-dorsal elevation of the epidermis overlies the dorsal nerve cord (Fig. 4). This ridge is less evident in the abdominal region.

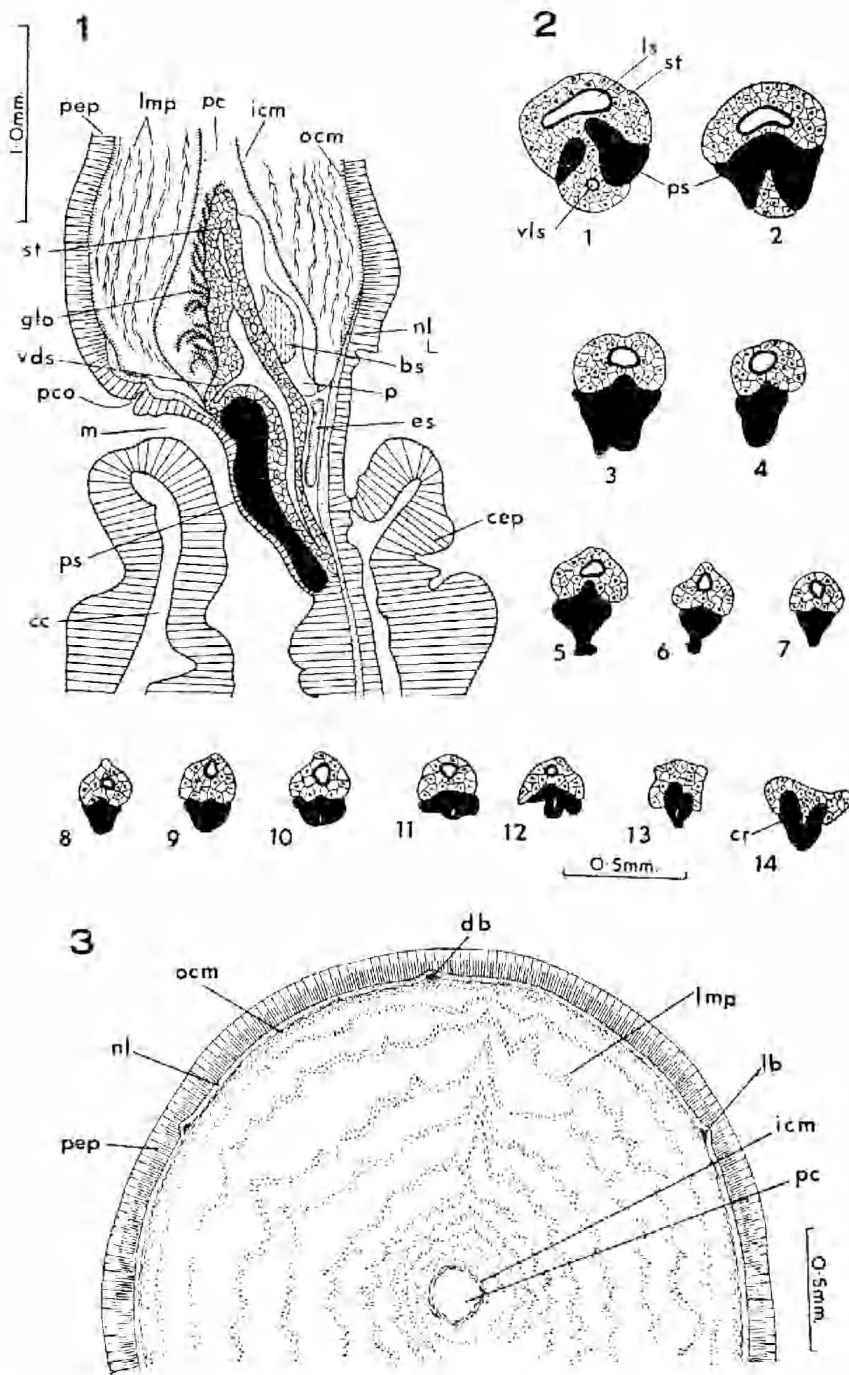


Fig. 1.—Longitudinal sagittal section of the base of the proboscis. bs., blood sinus; cc., collar coelom; cep., collar epidermis; es., end sac; glo., glomerulus; icm., inner circular muscle layer of proboscis; lmp., longitudinal muscles of proboscis; m., mouth; nl., nerve layer; ocm., outer circular muscle layer of proboscis; p., pericardium; pc., proboscis coelom; pco., pericardial ciliary organ; pep., proboscis epithelium; ps., proboscis skeleton; st., stomochord; vds., ventral diverticulum of stomochord.

Fig. 2.—1 to 14, Serial sections of stomochord and proboscis skeleton at about 0.05 mm. intervals. cr., crura of proboscis skeleton; ls., lumen of stomochord; vls., lumen of ventral diverticulum of stomochord; other guide letters as in previous figure.

Fig. 3.—Transverse section of proboscis. db., dorsal blood vessel of proboscis; lb., lateral blood vessel; other guide letters as in previous figures.

About two millimetres behind the last pair of gill pores the paired intestinal pores can be seen on the dorsal surface. They form two rows (Figs. 7 and 8), one on each side of the mid-dorsal line which diverge at an angle of thirty-five to forty degrees from the mid-line. Six to eight apertures appear on each side. In *S. kowalevskyi* (van der Horst, 1927-39) it is reported that the posterior of the four to six pairs of pores present are further from the mid-line than are the anterior ones. Through the kindness of Prof. F. W. Rogers Brambell, the author has been able to examine some specimens of *S. cambrensis*. In these, the five to seven pairs of patent pores form lines parallel to the mid dorsal line. A similar condition obtains in *S. inhacensis* (Kapelus, 1936). No descriptions of the external appearance of the intestinal pores seem to be available for other members of the genus.

Ventrally, in the trunk region, the main longitudinal musculature of the body is readily identifiable by its fine transverse striations. In the anterior branchial region, this musculature, though thicker in the ventral region, extends upwards in the lateral body walls nearly to the level of the gill pores (Fig. 4). Farther back, it becomes more concentrated ventrally so that at the posterior end of the branchial region and in the oesophageal region (Fig. 8) it forms two conspicuous ventro-lateral ridges which taper away towards the end of the genital region but are still visible in the abdominal region (Fig. 5). The ventral nerve cord can be seen medially between the lateral muscle masses throughout the length of the trunk.

The width of the intestinal region of a freshly caught specimen is, near its anterior end, little more than half that of the genital region even though it may be distended by its content of sand and shell-grit. It tapers gradually to about half this width near its posterior extremity. The ventral longitudinal muscle ridges, though diminishing in size, are visible throughout its length.

The epidermis of the trunk region is mainly glandular and can be divided into three different types. That in the vicinity of the gill pores is smooth and similar to that described for *S. cambrensis* and *S. horsti*. That covering the ventral and (in the anterior branchial region) lateral longitudinal muscle bands has fine transverse elevations which have already been noted above; while that on the remainder of the dorsal surface, on the genital ridges and on the lateral body walls, is raised into small, transversely arranged elliptical eminences (Figs. 5 and 7).

III. INTERNAL ANATOMY

The epidermis of the proboscis is between 0.1 and 0.2 mm. thick (Figs. 1 and 3). The nerve layer which lies immediately under it shows a slight dorsal thickening which, however, is much less well developed than is the corresponding structure in *S. cambrensis* and *S. horsti*. This may be associated with the slighter development of the dorsal groove of the proboscis in *S. apuntensis*. The dorsal (subneural), the two lateral and the ventral blood vessels lie between the nerve layer and the outer layer of circular muscles. The latter is about equal in thickness to the nerve layer and must be capable of very forceful contractions as is indicated by its ability to autotomise portions of the proboscis. The main bulk of the proboscis tissues is made up of longitudinal muscle fibres which are arranged in concentric rings, each ring being separated from its neighbours by a layer of loose connective tissue. At least nine or ten of these rings are apparent in all specimens examined (Fig. 3) and occasionally there are indications of an eleventh incomplete ring represented by a number of scattered longitudinal fibres which lie close to the inner layer of circular muscle fibre which line the proboscis coelom. Seven to ten such concentric rings have been described in *S. mereszkowskii* and nine or more in *S. horsti*. Towards the posterior end of the proboscis, the inner rings become indistinct and disappear so that at the level of the anterior extremity of the proboscis complex, only five or six of them are readily apparent. The proboscis coelom extends nearly to

the anterior extremity of the organ. The glomerulus (Fig. 1) surrounds the anterior extremity of the stomochord but farther back it is found only ventrally and laterally to the stomochord.

The stomochord is fairly straight and bluntly rounded anteriorly. In much contracted specimens, however, it may be considerably buckled dorso-ventrally. It has a well-developed ventral diverticulum (Fig. 1) which is supported by the bifid tip of the proboscis skeleton (Fig. 2 (1)). The short, blunt prongs coalesce dorsally so that a ventral groove is formed in the skeleton (Fig. 2 (2) and (3)) in which lies the backwardly directed tip of the ventral diverticulum. The body of the skeleton narrows to become quite slender in its mid-region but mid-dorsally in its anterior part it bears a distinct ridge which penetrates the body of the stomochord (which lies immediately above it) in its mid-ventral line (Fig. 2 (3), (4) and (5)). In the hinder part of the body of the skeleton, lateral wings are slightly developed (Fig. 2 (11) and (12)), but these disappear before the skeleton bifurcates to form the crura (Fig. 2 (14)). The crura pass upwards, one on each side of the junction of the stomochord with the lining of the buccal cavity and then arch outwards, backwards and downwards in the wall of the buccal cavity. They extend about halfway along the length of the collar and embrace slightly more than half of the circumference of the buccal cavity. The proboscis skeleton has no hard, central concretions such as occur in some specimens of *S. cambrensis*, nor have such concretions been noted in the branchial skeleton.

Spengel (1893) recognised five transverse zones in the collar epidermis of enteropneusts, each zone being characterised by certain cell structures and staining propensities. In *S. apantesis* all five zones are clearly distinguishable (Fig. 6). The first, the anteriormost, is a fairly low epithelium of ciliated cells which stain lightly with Ehrlich's haematoxylin. This zone covers the anterior flange of the collar. The second zone, which is nearly as broad as the other four put together, contains much material which stains heavily with haematoxylin. Anteriorly, where it abuts on the first zone, its cells are low but they increase in height in the middle region to shorten again towards the hinder margin. Near its anterior margin there is a circular furrow whose depth varies considerably in relation to the degree of longitudinal contraction of the collar. The third zone consists of narrow, elongate cells in which material which stains heavily is concentrated towards their bases. This material does not stain quite as heavily as does that of the second zone. The fourth zone is the narrowest and forms the white line on the collar referred to previously. It bears a deep furrow and its cells contain relatively few deeply-staining particles towards their bases. The fifth zone, like the first, is ciliated but forms a much higher epithelium. It forms the posterior flange of the collar which overhangs the beginning of the branchial region.

The general arrangement of these zones is similar to that in *S. carabaeus* (van der Horst, 1927-39) and *S. kowalevskii* (Agassiz). In both these species the five zones are distinguishable. In *S. cambrensis*, the third and fourth zones are not readily distinguishable while in *S. horsti* they are indistinguishable. In *S. inhaensis* (Kapelus, 1936) none of the five zones is clearly demarcated.

The number of pairs of gill pores varies between thirty and forty-five. This number is less than is found in most other members of the genus. *S. gurneyi* approaches it most closely with forty to sixty pairs. The number of pairs of gill pores in the remaining species are given in the list of distinguishing features of the different species at the end of this article. The detailed histology of the branchial region shows no special distinguishing features. In transverse section the branchial portion of the pharynx is seen to be about equal in extent to the non-branchial (food-groove) portion (Fig. 4).

The first genital pouch appears in about the mid-branchial region. Mature oocytes (measured on fixed material) are about $310\ \mu$ long and about $285\ \mu$

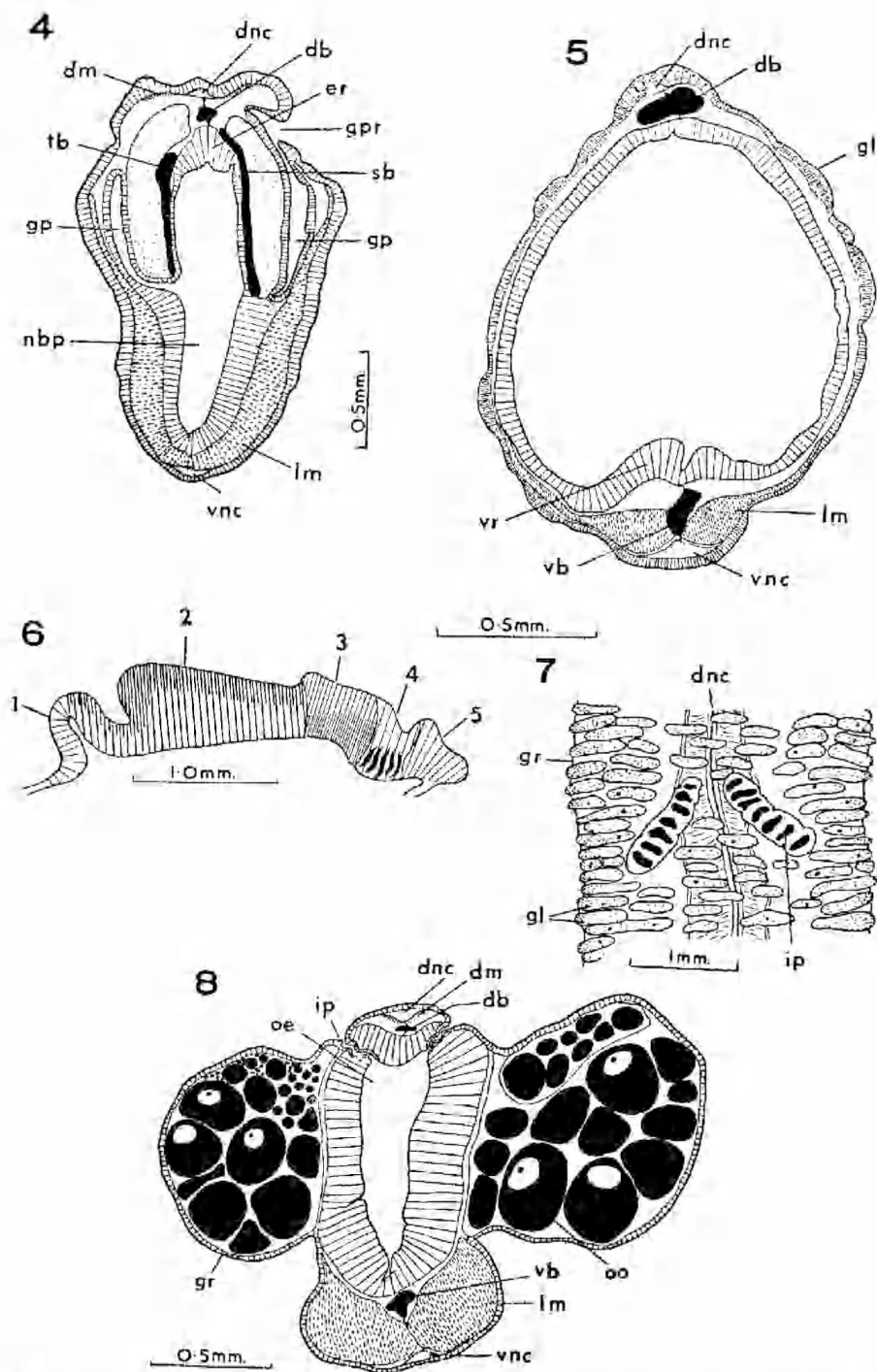


Fig. 4.—Transverse section in branchial region. db., dorsal bloodvessel; dnc., dorsal longitudinal muscle of trunk; dnc., dorsal nerve cord; dm., dorsal longitudinal muscle of trunk; dnc., dorsal nerve cord; er., epibranchial ridge; gp., gill pouch; gpr., gill pore; lm., longitudinal muscles of trunk; nbp., non-branchial portion of pharynx; sb., skeleton of gill septum; tb., skeleton of gill tongue; vnc., ventral nerve cord.

Fig. 5.—Transverse section of abdominal region. gl., glandular eminence; vb., ventral bloodvessel; vr., ventral ridge in gut epithelium; other guide letters as in previous figures.

Fig. 6.—Sagittal section of collar epidermis. 1 (anterior) to 5 (posterior), zones of collar epidermis.

Fig. 7.—Dorsal surface of oesophageal region showing arrangement of intestinal pores. gr., genital ridge; ip., intestinal pore; other guide letters as in previous figures.

Fig. 8.—Transverse section of second region of oesophagus. oe., lumen of oesophagus; oo., oocyte; other guide letters as in previous figures.

broad. They are thus intermediate in size between those of *S. cambrensis* ($400\ \mu$ by $300\ \mu$) and *S. kowalewskii* ($375\ \mu$) on the one hand and *S. huxleyi* ($230\ \mu$ by $170\ \mu$) and *S. otagoensis* ($250\ \mu$) on the other. Some six to ten mature oocytes appear in one transverse section as well as a larger number of immature ones. The latter are usually located medially and dorsally in the ovary, that is in the region of the genital pore, while the mature oocytes occupy a more central or ventral position (Fig. 8).

The oesophagus has the usual three regions. The first of these has an epithelium of moderate thickness which is very much folded and is histologically similar to that of the ventral, non-branchial, part of the pharynx. The second region has a thicker epithelium (Fig. 8) and it is into dorso-lateral grooves in this region that the intestinal pores open. There are six to eight pairs of these, there being no rudimentary pores such as appear in *S. cambrensis*. The third region of the oesophagus has a lower epithelium than the first region and this merges imperceptibly into the hepatic region, which, as in other members of the genus, is indistinguishable externally. The gut in the abdominal region (Fig. 5) has a broad lumen and thin walls. Ventro-laterally the walls are thickened to form two marked parallel ridges, separated by a deep mid-ventral furrow. The ventral musculature in this part of the body is much reduced and there are only very slight traces of the fine bands of dorsal longitudinal muscles which are apparent throughout the branchial and oesophageal regions.

IV. SPECIFIC CHARACTERS AND COMPARISON WITH OTHER SPECIES

The specific characters of *Saccoglossus apantesis* are listed below:

- (a) There are between thirty and forty-five pairs of gill clefts.
- (b) The gonads start in the mid-branchial region and form marked dorso-lateral ridges.
- (c) The oocytes are nearly spherical, measuring about $310\ \mu$ by $285\ \mu$.
- (d) The ventral, longitudinal muscles of the trunk form distinct ventro-lateral ridges in the posterior branchial and oesophageal regions.
- (e) There are six to eight pairs of intestinal pores.
- (f) The epidermis of the collar has five distinct zones, the second of these being almost equal in extent to the remaining four added together.
- (g) The dorsal proboscis groove is but slightly developed in the posterior quarter of the proboscis.
- (h) The longitudinal musculature of the proboscis is arranged in at least nine or ten complete concentric rings.
- (i) The stomochord has a ventral diverticulum which is directed slightly backwards and is partially grasped by the bluntly bifid tip of the proboscis skeleton.
- (j) The crura of the proboscis skeleton extend about halfway along the length of the collar and embrace slightly more than half the circumference of the buccal cavity.

S. apantesis is the fifteenth member of the genus to be described. It can be distinguished from the other species on the following combinations of characters:

- S. sulcatus* (Spongel). Loc. Japan. Deep dorsal sulcus on the proboscis giving it a crescentic cross section; ten to eleven pairs of gills.
- S. otagoensis* (Benham). Loc. New Zealand. Deep dorsal groove on the proboscis; ten to fifteen pairs of gill pores; longitudinal muscles of the proboscis in three or four concentric rings; gonads extend anteriorly to the level of the fourth gill pore; one pair of intestinal pores.
- S. pygmaeus* (Hinrichs and Jacobi). Loc. Heligoland. Nine to twenty-two pairs of gill pores; longitudinal muscles of proboscis not in concentric rings;

- gonads begin at posterior extremity of the branchial region; one pair of intestinal pores; very small form, about three centimetres long.
- S. gurneyi* (Robinson). Loc. Suez. Collar nearly twice as broad as long; longitudinal muscles of proboscis not in concentric rings; forty to sixty pairs of gill pores; median proboscis pore; gonads begin immediately behind the collar; intestinal pores absent (?).
- S. carabaeus* (van der Horst). Loc. West Indies. Longitudinal muscles of the proboscis not in concentric rings; median proboscis pore; more than fifty pairs of gill pores; gonads begin between the fourth and fifth gill pores.
- S. bournei* (Menon). Loc. Madras. Longitudinal muscles of the proboscis not in concentric rings; crura of proboscis skeleton extend to the hinder end of the collar; ventral musculature of the trunk region not especially thick; gonads begin immediately behind the collar.
- S. pusillus* (Ritter). Loc. California. Crura of the proboscis skeleton extend to the hinder end of the collar and embrace three-quarters of the circumference of the buccal cavity; about sixty pairs of gill pores; one pair of intestinal pores.
- S. mereschkowskii* (Nic. Wagner). Loc. North-Eastern Russia. Fifty pairs of gill pores; endplate of the proboscis skeleton bears a long dorso-median spine; collar epidermis very thick (0.5 mm.).
- S. inhacensis* (Kapelus). Loc. South-East Africa. Eighty-two or more pairs of gill pores; longitudinal muscles of the proboscis not in concentric rings; gonads begin at the level of the fourth gill pores; four pairs of intestinal pores, the first of which has four internal openings.
- S. kowalevskyi* (A. Agassiz). Loc. Atlantic coast of the U.S.A. A hundred pairs of gill pores; genital folds begin one millimetre behind the collar; only four or five rings clearly visible in the longitudinal muscle of the proboscis; four to six pairs of intestinal pores.
- S. ruber* (Tattersall). Loc. Western Ireland. Longitudinal muscles of the proboscis not in concentric rings; no genital or muscular ridges on the trunk; fifty-six to sixty-four pairs of gill pores.
- S. serpentinus* (Assheton). Loc. Scotland. Very long proboscis and body, trunk circular in cross section, without genital or muscular ridges; sixty pairs of gill pores; longitudinal muscle of proboscis not in concentric rings.
- S. cambrensis* (Brambell and Cole). Loc. North Wales. Trunk circular in cross section without genital or muscular ridges; sixty to ninety pairs of gill pores; four to six ill-defined concentric rings in the peripheral part of the longitudinal musculature of the proboscis; eight to twelve pairs of intestinal pores, the first three to five pairs being rudimentary. Intestinal pores arranged parallel to the mid-dorsal line.
- S. horsti* (Brambell and Goodheart). Loc. Southern England. Dorsal and ventral grooves present on the proboscis throughout its length; gonads begin within one millimetre of the collar; one hundred to one hundred and forty pairs of gill pores; four to eight pairs of intestinal pores.

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